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SPECIATION IN THE GENUS *OCHTHOECA* (AVES: TYRANNIDAE)[1]

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ABSTRACT. The nine Chat-Tyrants are small tyrannid flycatchers occurring in the Andes from Colombia and western Venezuela south to Bolivia and extreme northern Chile. Most of the species are divided into numerous isolated races. There are several distinct species-groups, and the species are highly sympatric. The complicated ranges appear to have arisen during the final three Pleistocene glacial periods in the northern Andes. During glacial peaks, the then-existing species dispersed over wide ranges. They were divided during the subsequent interglacials. The three periods of dispersal and subsequent splitting first isolated the species-group precursors, then the species themselves, and finally the races of each species. The many isolated races of each species today are separated by geographic and vegetational barriers which probably affect a number of other montane species as well.

INTRODUCTION

Several recent studies (B. Vuilleumier, 1971; F. Vuilleumier, 1969, 1970) have revealed consistencies in the ranges and speciation patterns of the fauna of the South American Andes. The patterns indicate that a large number of Andean species originated and diverged in conjunction with the periodic glaciations of the Quaternary. Alternating glacial advances and retreats resulted in the complex sympatry between related species occurring there today.

The avian genus *Ochthoeca* reflects this type of complex sympatry. Eight of its nine species have widely separated races, and although several species occur throughout the central and northern Andes, others are confined to smaller areas. Sympatry among species in the genus is considerable.

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O. CINNAMOMEIVENTRIS

O. RUFIPECTORALIS

O. FRONTALIS

O. FUMICOLOR

Figure 1. Four members of the genus *Ochthoeca*. Species-groups *diadema* and *oenanthoides* are represented by *O. frontalis* and *O. fumicolor*, respectively. About two-thirds life size.

Known collectively as the Chat-Tyrants, all species are tree- or shrub-inhabiting flycatchers of the middle- and high-altitude Andes. They occur in the upper subtropical, temperate, and páramo zones from the mountains of western Venezuela and Colombia south to western Bolivia and extreme northern Chile. Members of the genus have been collected at altitudes from 500 to 4314 meters, and the average for the group is slightly over 2700 meters. They are small, generally chunky and large-headed flycatchers, and all have a conspicuous supraloral stripe, or "eyebrow," varying in length and color (see Fig. 1). Their chief mode of prey-catching is gleaning insects from the vegetation, though several species also sit on conspicuous perches and hawk insects from the air (F. Vuilleumier, 1971). All species are nonmigratory and, with one apparent exception, they are common within their respective ranges.

The ranges of each species, plotted from their collection localities, are shown in Figure 2. Based on these present ranges and on the Andean glacial events during the Quaternary, I shall propose here a sequence of speciation for the group.

The Genus

The genus *Ochthoeca*, as recognized by de Schauensee (1966), contains the nine species listed below. Two species are quite distinct from the others and have widespread ranges. The remaining seven have been placed in two species-groups by F. Vuilleumier (1971).

O. cinnamomeiventris
O. rufipectoralis
diadema species-group
O. diadema
O. frontalis
O. pulchella
oenanthoides species-group
O. oenanthoides
O. fumicolor
O. leucophrys superspecies
1. *leucophrys*
2. *piurae*

F. Vuilleumier considered *O. pulchella* and *O. frontalis* as members of a superspecies within the *diadema* species-group. Although they are very similar, differing chiefly in the amount of yellow in the eyebrow, both species have been collected at

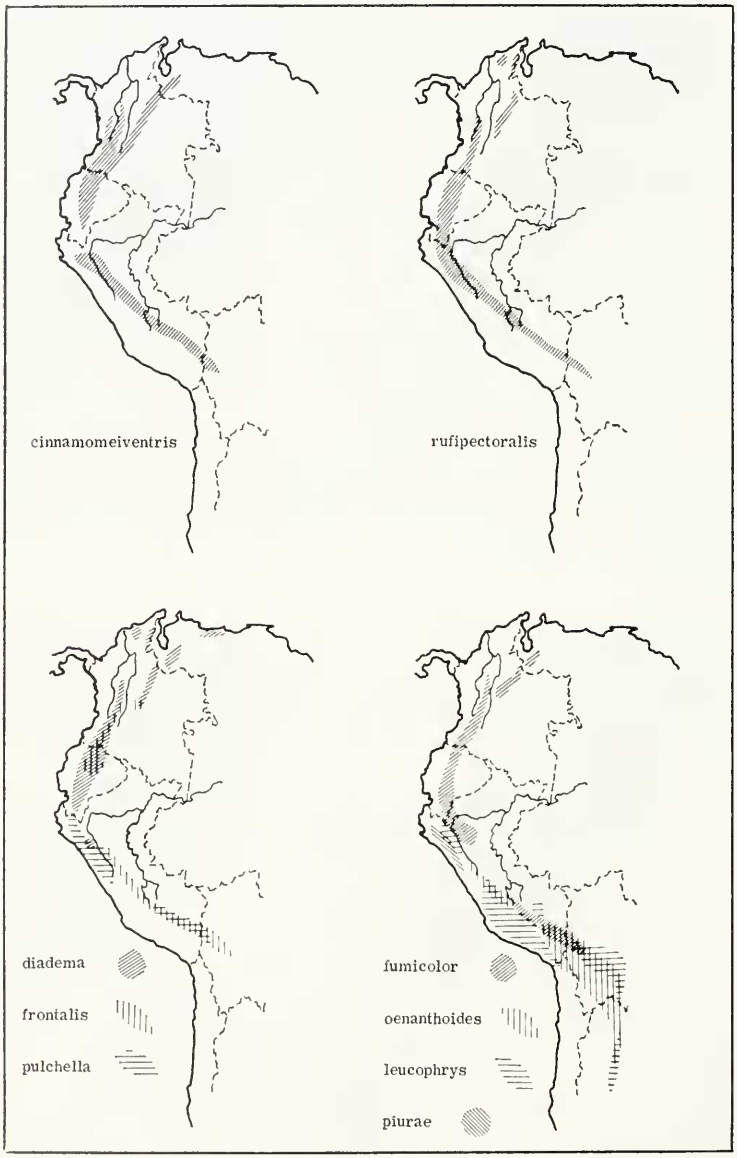


Figure 2. Ranges of species in *Ochthoeca*. The *diadema* and *oenanthoides* species-groups are shown on the lower left and lower right, respectively.

each of four localities, and their ranges show considerable overlap south of the Marañón River. I shall, therefore, treat them as sibling species within the group.

One species, *cinnamomeiventris*, occurs in the moist forests of the upper subtropical and temperate zones. Its dark coloration is adapted to these dense, wooded habitats. Its bill is the broadest and shortest of the genus, reflecting its diet of aerial insects captured by hawking. *O. rufipectoralis* and the *diadema* species-group inhabit open forests of the temperate zones. Their bills are also short, but all are much thinner than that of *cinnamomeiventris*. *O. diadema* is the only species whose plumage is largely green. The *oenanthoides* species-group contains forms frequently found over 4000 meters. *O. fumicolor* lives in moist páramo habitats, while *oenanthoides* and the *leucophrys* superspecies occur in the dry puna scrub and grasslands (F. Vuilleumier, 1971). Members of this group have long, thin bills adapted to their diet of insects gleaned from the vegetation. All have significantly larger bodies than the other *Ochthoeca* species, with relatively longer wings and tails. *O. leucophrys* is predominantly grey, while the other two are buffy brown.

Pleistocene Climatic Influences

The zoogeographic history of these species seems closely related to the periodic altitudinal lowering of their habitats during the Quaternary glaciations. Glacial climates affected the forest- and grass-life zones in two ways. First, the limits of each were lowered, creating connections or closer proximity between previously isolated habitats. During maximum glaciation, the life zones were lowered sufficiently to become nearly continuous along the entire mountain chains (B. Vuilleumier, 1971). Second, the valleys and lower mountain areas became more humid as the ice and glacial lakes surrounded them. This again resulted in greater proximity between the formerly higher and isolated humid life zones. During the glacial maxima, the lowering of the habitats permitted many avian species to colonize through the northern mountain chains along a north-south axis. During interglacial periods the life zones retreated to higher altitudes, thereby splitting again into isolated "islands." The deep valleys became dry, further decreasing the potential for gene flow between neighboring high-altitude populations. Thus a species whose range had been widespread and nearly continuous during maximum glaciation divided during the subsequent interglacial. New races and species evolved as a result.

Within the central and northern Andes, two particular climatic features affected speciation in high-altitude populations. First, the western slope from southern Ecuador through Peru and northern Chile now receives very little rainfall. Presumably this was the same in the past, and the area remained generally unavailable to the forest-inhabiting *Ochthoeca* species. Only one species, *leucophrys*, occurs in this arid region today. Second, two large areas of low, dry vegetation occur within the range of this genus. The first is the low, semi-arid valley of the upper Magdalena River, which lies between the Eastern and Central Cordilleras of Colombia, creating a significant barrier between a number of montane taxa on either side (F. Vuilleumier, 1969). Five *Ochthoeca* species now occur in northern Colombia and northwest Venezuela. Only that species inhabiting the lowest altitudes does not show a major break and/or subspecific differentiation in this area. A second, equally effective barrier occurs in the region of the upper Marañón River in northern Peru. The low mountains in this area create a wide break between the extensive high-altitude regions of Peru and Ecuador. The ranges of all nine *Ochthoeca* species reach this divide, and six show major breaks at the barrier. Furthermore, evidence exists that warmer Pleistocene interglacial temperatures resulted in even drier conditions still less favorable to alpine life than today's climate (B. Vuilleumier, 1971). Hence these dry barriers isolated populations more effectively in the past than they do today. These two major divides thus created three large, separate areas of montane conditions north of Bolivia which appear to have been the primary centers for speciation in *Ochthoeca*, and certainly for other species as well.

Speciation in Ochthoeca

Geologists recognize four major world-wide glacial advances during the Pleistocene (*e.g.*, Leet and Judson, 1971), but the first had relatively less effect on the northern Andes, since they were the last to attain their present height (B. Vuilleumier, 1971). Data on high-altitude species in the northern Andes indicate that they were derived predominantly from central Andean birds (F. Vuilleumier, 1970). Species originating in these central mountains dispersed northward during the three major glacial periods affecting the northern mountains. The precursor of the genus *Ochthoeca* seems therefore to have originated in the central Andes, and became isolated during the first Pleisto-

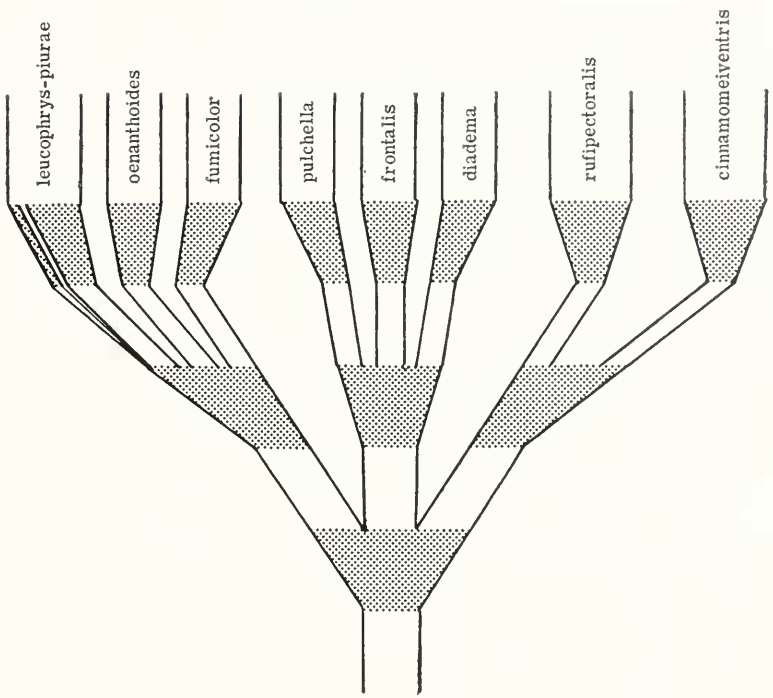


Figure 3. Schematic evolution of the genus through time, from its ancestral stock. Shaded areas show dispersal periods during the final three glaciations; unshaded areas represent interglacial periods, when isolated populations differentiated into new forms.

cene interglacial period. As are most species today, this was probably an open-forest bird. The occurrence of seven of today's nine species in northwestern Bolivia and southern Peru further indicates that the area was probably suitable to the precursor.

The development of the modern genus from this precursor is suggested by the structure of the group as a whole. The existence of clear-cut species-groups, the subdivision of the groups into component species, and the species' divisions into morphologically distinct races indicate three separate occasions of dispersal each followed by isolation. In the first period, the parent species was split into species-group precursors, which in turn split into their component species following the second dispersal period.

Finally, after the third period, each species was broken into the isolated populations found today. These three dispersal periods correspond to the three glaciations following the isolation of the progenitor early in the Pleistocene. This pattern is outlined in Figure 3. A detailed sequence for this speciation will now be presented.

During the first of the three glaciations, the parent species was probably able to colonize northward over the entire Andean chain. Colombia's Eastern Cordillera had by this time gained its present altitude and could support alpine life, particularly during the cold, damp glacial period. At this time there was sufficient gene flow throughout the range to inhibit differentiation and the population remained a single species.

Upon glacial retreat, the two major geographic barriers, the Magdalena and the Marañón valleys, became effective. As illustrated in Figure 4a, the original species was split into three populations that formed the parent stocks of the two species-groups and the precursor to the remaining two species. The southernmost population, in the highest mountain areas, gave rise to the highest-altitude species-group. This precursor shall be referred to as "oenanthoides."[1] This conclusion is further strengthened by the generally southern ranges of these species. While this form was confined to Peru and Bolivia, forest birds

[1]To avoid confusion between these primitive taxa and the modern species to which they gave rise, the precursors will be called by their species-group name, within quotation marks. Hence "oenanthoides" eventually gave rise to the species now within the *oenanthoides* species-group.

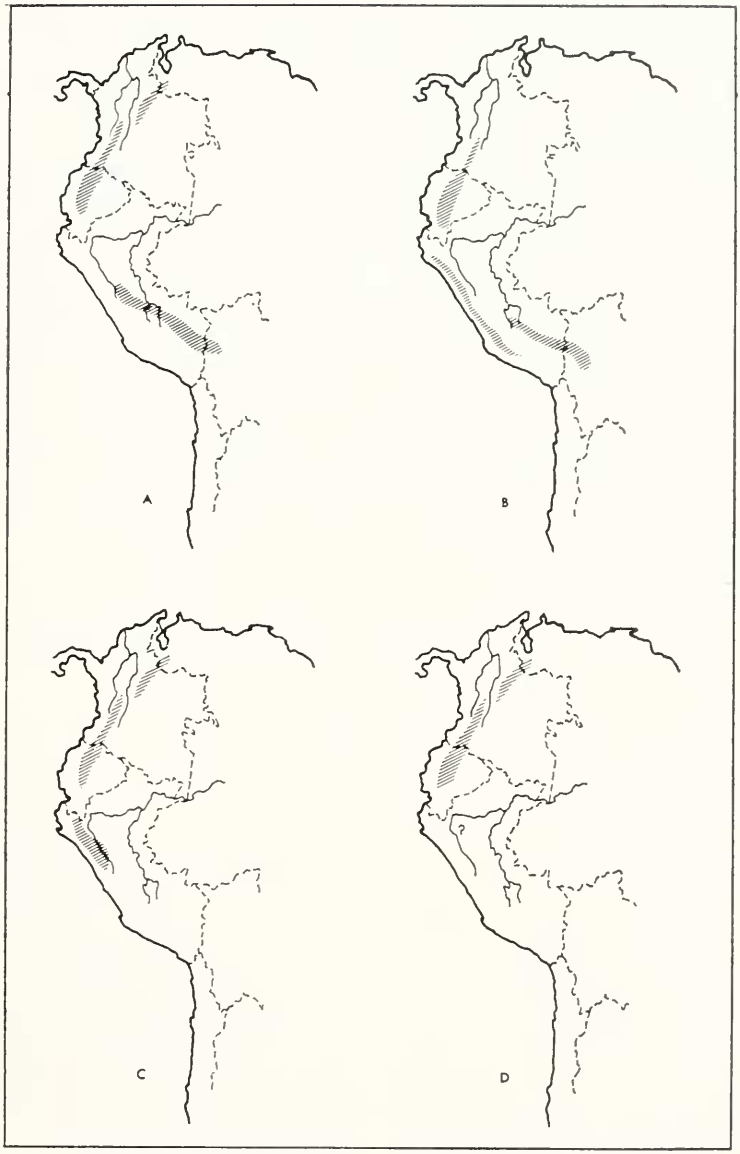
Figure 4. (A) Three populations isolated after the Mindel (second) Pleistocene glaciation; "diadema" (north) and "oenanthoides" (south) gave rise to the respective species groups; "rufipectoralis" (central) differentiated as shown in 4(D).

(B) Status of "oenanthoides" during and following the Riss (third) glaciation; *leucophrys* (west) and *oenanthoides* (east) were separated by glacial ice and lakes. *O. fumicolor* differentiated in the north.

(C) Isolation of *diadema* (north), *frontalis* (central), and *pulchella* (south) from "diadema" following the Riss glaciation.

(D) Isolation of *cinnamomeiventris* east of the Magdalena River following the Riss glaciation. *O. rufipectoralis* (central) may have ranged south of the Marañón River by this time.

Various races have now differentiated following the dispersal of the species during the Würm (final) glaciation.


A
B
C
D

in western Ecuador and Colombia differentiated into "rufipectoralis." The population that was isolated in the Eastern Cordillera of Colombia became "diadema." These latter two forms probably remained relatively undifferentiated until the succeeding glaciation brought them into secondary contact, since even today they apparently share similar habitats.

The second glacial episode again resulted in range extensions along the lower valleys. An important occurrence during this period is illustrated in Figure 4b: "oenanthoides," which was evolving into a higher-altitude, páramo-inhabiting species, extended through the central and northern mountains. Its range seems to have been divided during the glacial peak by the extensive ice and glacial lakes that capped the highlands of Peru and Bolivia in complex patterns (B. Vuilleumier, 1971). Thus at least three populations were isolated during this glaciation, as a result of their high-altitude requirements. Restricted by the ice to a portion of the western slope, *leucophrys* developed into a puna-inhabiting species. *O. oenanthoides* differentiated to the east, and the two apparently exclude each other over much of their ranges, for sympatry today remains fairly small; they still reflect somewhat these primitive ranges. *O. piurae* also probably speciated at this time on an isolated puna region in extreme northwestern Peru, never drifting far enough from *leucophrys* to permit extensive sympatry after the glacial retreats.

Figure 4c illustrates the probable spread and differentiation of "diadema" into the species of that group. Again the two barriers created three surviving, isolated populations, which evolved into *diadema* in the north, *frontalis* in the central mountains, and *pulchella* south of the Marañón. Characters shared by these species are nearly identical wing, tail, and bill measurements, wingbars, and bright yellow in the eyebrow, as well as smoky-grey crowns and backs; their close relationship is quite clear. Their current ranges reflect the three primitive ranges, with one exception: the range of *frontalis* now extends southward to overlap that of *pulchella*. To judge from collection data, however, *frontalis* appears less common within this southern range extension. The frequency of *pulchella* south of the Marañón and its total absence farther north indicate that *frontalis* did achieve species rank in the north and move south into *pulchella*'s range.

The second glaciation allowed the expansion of "rufipectoralis" along the forests of the northern Andes, possibly through-

out the range of the genus. When the ice retreated, two populations were separated. In the forests east of the Magdalena River, *cinnamomeiventris* differentiated, and in the central Andes, *rufipectoralis* reached species rank. This pattern is suggested by the large gap in the current range of the latter species across the Magdalena. This break is not present in the range of *cinnamomeiventris*, which adapted to the moist forests at a lower altitude in the Eastern Cordillera. Furthermore, the relative frequencies of the two species follow this pattern — *cinnamomeiventris* is common in the north and occurs only at scattered localities south of Colombia. *O. rufipectoralis* is much more common in the south though it has established small populations in the north, where *cinnamomeiventris* originated. Their close relationship is supported by their sharing of the white eyebrow and the conspicuous rufous-chestnut breast band. *O. cinnamomeiventris* appears to be a darkened form of *rufipectoralis* adapted to forest habits (see Figure 1). Their morphological and ecological differences certainly increased upon secondary contact, and both species eventually dispersed throughout the range of the genus. Their phylogenetic relationship appears to be analogous to that of the two species-groups. Their status as taxonomically distinct species arose from their more significant divergence following the second glaciation.

Thus all current species were present at the onset of the final glaciation. Their ranges had already overlapped in several regions, and they probably had become well differentiated. During this glaciation the species colonized new areas as far as suitable habitat and competition with congeners permitted. The northeastern species, *diadema* and *cinnamomeiventris*, moved south, *diadema* stopping where *pulchella* was established. Many populations seem to have crossed the Marañón to invade the moist eastern slopes of Peru, resulting in the seven species occurring there today. *O. leucophrys*, a strictly high-altitude species, crossed to the east and spread south into Argentina. Upon glacial retreat this resulted in a series of isolated populations stretching southward along the mountains at progressively lower altitudes that coincided with the preferred habitat. In short, each species spread to its ecological limits and was subsequently split by the final warming and drying of the valleys. Hence the morphological isolates recognized today give evidence for the geographic barriers that split these last major glacial range expansions.

Current Speciation

Isolated races of each species now exist in regions which, following the last glaciation, became sufficiently separated to limit gene flow between them. Several interesting exceptions are worthy of note.

The relative scarcity of *O. frontalis* (I found only twenty localities recorded in the literature) makes meaningful discussion of its subspecific ranges difficult. The apparent large break in its distribution in northern Peru seems insufficient to isolate the populations on either side, as both are apparently the same race (Carriker, 1933; Zimmer, 1937). It appears, therefore, that the gap is a product of the rarity of the species, rather than a genuine absence throughout the region.

The subspecific continuity of *O. fumicolor* across this same low divide is also confusing, for the species normally occurs at altitudes well over 3000 meters. In contrast to *O. frontalis, O. fumicolor* is extremely common in the north-central Andes; apparently the few small isolated páramos within the divide permit the maintenance of gene flow across it. Collection localities from north to south through the divide are: Bestión (3100 m), Taraguarcocha (3200 m), El Tambo (2900 m), Cutervo (3000 m). Hence certain sufficiently common species apparently have the potential for gene flow across this divide.

Among other species, in areas lacking any major geographic barriers, several subspecific discontinuities are found which would seem to be the result of habitat breaks not marked on vegetation maps. In one such area, *O. frontalis, O. cinnamomeiventris,* and *O. rufipectoralis* each split into different races on either side of the extreme upper Marañón, while higher altitude species do not. Excessive taxonomic splitting of clinical differentiation may cause these anomalies.

In general, the modern ranges of the species, with their many isolated races, provide accurate evidence of currently isolated vegetation zones. Such regions, as indicated also by B. Vuilleumier (1971), are presumably equally important in many other upper montane species. These regions, some of which may be areas of current or future speciation, are separated by the geographic barriers listed below. The *Ochthoeca* species split apart by the barriers are listed under each.

1. Huallaga Valley, southern Peru
   fumicolor, leucophrys, pulchella

2. Marañón Valley and low Peruvian mountains
   cinnamomeiventris, diadema
3. Upper Magdalena Valley, northern Colombia
   fumicolor, diadema, frontalis, rufipectoralis
4. Cristóbal Valley, separating mountains of Mérida, Venezuela, from the Eastern Cordillera
   fumicolor, cinnamomeiventris, diadema
5. Yaracuy River valley, isolating the northern coastal mountain ranges of Venezuela
   diadema
6. César Depression, isolating Nevada de Santa Marta
   diadema, rufipectoralis
7. Upper Rio Catumbo depression, separating the Perija Ridge from the Eastern Cordillera
   diadema, rufipectoralis

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